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Studies on the Biology of Barnacles: Parasites of *Balanus eburneus* and *B. balanoides* from New York Harbor and a Review of the Parasites and Diseases of Other Cirripedia[1]

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(Plate I)

Three species of organisms previously reported as predators or as parasites of barnacles and two commensal peritrichs have been found in populations of *Balanus eburneus* and *Balanus balanoides* occurring on the rock jetties from Sea Gate and immediately adjacent to the Osborn Laboratories of Marine Sciences at Seaside Park, Coney Island, New York City, respectively. The species found were *Cephaloidophora communis* (Protozoa: Sporozoa: Gregarinida: Eugregarinina: Cephalinoidea: Cephaloidophoridae) from the intestine of *Balanus eburneus; Epistylis horizontalis* and *Epistylis nigrellii* (Protozoa: Ciliophora: Ciliata: Peritrichidae) from the branchial lamellae of *Balanus balanoides* and *B. eburneus,* respectively; *Stylochus ellipticus* (Platyhelminthes: Turbellaria: Polycladia: Acotylea: Stylochidae) from the internal wall of the opercular valves of *Balanus eburneus* attached to *Mytilus edulis;* and metacercariae, possibly of *Maritrema arenaria* (Trematoda: Digenea: Microphallidae), on the external gut wall and other tissues of *Balanus balanoides.* The presence of these organisms in local barnacles represents a new geographical record. These and their effects on the host are briefly described together with a review of the literature on other parasites and diseases of barnacles.

Introduction

There is very little information in the literature on the diseases and parasites of Cirripedia, and apparently only the members of the Balanidae have been investigated with any degree of thoroughness. The most common group of parasites found in these sessile crustaceans are the Gregarinida (Protozoa: Sporozoa), fungal parasites, larval digenetic trematodes (metacercariae), and a single species (*Hemioniscida balani*) of parasitic isopod have also been reported. Some of these parasites may be more common than indicated in the literature. Studies in our laboratory have shown that one species of gregarine (*Cephaloidophora communis*) and the metacercaria of a microphallid trematode, together with a predatory turbellarian (*Stylochus ellipticut*) and a commensal peritrich ciliate (*Epistylis horizontalis*), occur in barnacles (*Balanus eburneus* and *B. balanoides*) in the New York area. These are reported below together with a review of the literature.

Gregarinida

Gregarines have been repeatedly observed in barnacles since they were first described by Kölliker in 1847; the most recent report deals with electron microscope studies on *Cephaloidophora communis* in the intestine of *Balanus tintinnabulum* (Reger, 1966). *C. communis* was first described in *Balanus improvisus, B. eburneus,* and *B. amphitrite* by Mawrodiadi in 1908, and has since been reported by several authors in other Balanidae. This species, together with *Pyxinioides bolitoides* in *Balanus nubilis* from the Pacific coast (see Table I), was recently discovered by the present investigators in *Balanus eburneus* collected on the jetties adjacent to the Osborn Laboratories of Marine Sciences. Since development occurs when the sporozoites penetrate the cells of the gut epithelium, some pathological effects (*e.g.* necrosis and desquamation) must occur in spite of the seemingly innocuity of the bioassociated sporadins (Pl. I, fig. 1). Barnes (1955) suggested that infections with gregarines have some profound effect on the

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TABLE I
PROTOZOA: GREGARINIDA

Host	*Parasite*	*Author*
Balanus pusillus	*Gregarina balani*[2,6]	Kölliker, 1847
Pollicipes polymerus	*Gregarina valettei*[7]	Nussbaum, 1890
Balanus improvisus	Unnamed gregarine	Solger, 1890
Balanus perforatus	*Nematoides fusiformis*[3]	Mingazzini, 1891
Balanus perforatus	*Nematoides fusiformis*	Labbé, 1899
Pollicipes cornucopia	*Nematoides fusiformis*	Labbé, 1899
Balanus improvisus	*Cephaloidophora communis*[7]	Mawrodiadi, 1908
Balanus eburneus	*Cephaloidophora communis*	Mawrodiadi, 1908
Balanus amphitrite	Unnamed gregarine	Mawrodiadi, 1908
Chthamalus stellatus	*Frenzelina chthamali*[4]	Léger and Duboscq, 1909
Chthamalus stellatus	*Cephaloidophora communis*	Léger and Duboscq, 1909
Balanus eburneus	Unnamed gregarine	Budington, 1910
Balanus amphitrite	*Pyxinioides balani*	Trégouboff, 1912
Balanus eburneus	*Pyxinioides balani*	Trégouboff, 1912
Balanus improvisus	*Cephaloidophora communis*	Trégouboff, 1912
Balanus tintinnabulum	*Cephaloidophora communis*	Trégouboff, 1912
Balanus amphitrite	*Cephaloidophora communis*	Ball, 1937
Balanus crenatus	*Cephaloidophora communis*	Henry, 1938
Balanus glandula	*Cephaloidophora communis*	Henry, 1938
Balanus cariosus	*Cephaloidophora communis*	Henry, 1938
Balanus nubilis	*Pyxinoides bolitoides*[5]	Henry, 1938
Balanus nubilis	*Gregarina spissa*	Henry, 1938
Balanus nubilis	*Cephaloidophora magna*	Henry, 1938
Balanus balanus pugetensis	*Cephaloidophora multiplex*	Henry, 1938
Balanus rostratus heteropus	*Cephaloidophora multiplex*	Henry, 1938
Balanus balanus pugetensis	*Pyxinoides pugetensis*[5]	Henry, 1938
Mitella polymerus	*Gregarina valettei*	Henry, 1938
Balanus eburneus	*Cephaloidophora communis*	Ball, 1950
Balanus balanoides	*Gregarina balani*	Ouspenskaia, 1960
Balanus amphitrite	*Cephaloidophora communis*	Heckman, 1961
Chthamalus stellatus	*Bifilida rara*	Tuzet and Ormières, 1964
Chthamalus stellatus	*Pyxinioides chthamali*	Tuzet and Ormières, 1964
Balanus tintinnabulum	*Cephaloidophora communis*	Reger, 1966
Balanus eburneus	*Cephaloidophora communis*	Arvy and Nigrelli (Present paper)
Balanus nubilis	*Pyxinioides bolitoides*	Arvy and Lacombe (recorded in present paper)
Balanus balanoides	*Epistylis horizontalis* Chatton[1]	Arvy and Batisse, 1968
Balanus eburneus	*Epistylis nigrellii*	Arvy and Batisse, 1968

[1] Arvy, and Batisse (in press) recently rediscovered the peritrich ciliate *Epistylis horizontalis Chatton* among the ovarian follicles in *Balanus balanoides* collected off the rock jetty adjacent to the Osborn Laboratories of Marine Sciences; they also reported a new species, *E. nigrellii,* from the gills of *B. eburneus* in the same locality.

[2] The barnacle parasites included in the *Gregarina* must be reclassified since the members of this genus are exclusively found in insects (Tuzet and Ormières, 1964).

[3] Sporocysts of *Gregarina* and *Nematoides* in Cirripedia are unknown.

[4] The name *Frenzelina* is now used for a testate sarcodina of the family Difflugiidae; *F. chthamali,* however, is a true gregarine that has been reclassified as *Cephaloidophora* and/or *Pyxinioides* (see Henry, 1938, for discussion of this species).

[5] Misspelling for *Pyxinioides,* the generic name created by Trégouboff (1912).

[6] Kamm (1922) believes that *Gregarina balani* is a synonym of *Pyxinioides balani* and redescribes *Cephaloidophora communis, Pyxinioides chthamali, Gregarina valettei,* and *Nematoides fusiformis* from various species of barnacles.

[7] Henry (1938) redescribes *Cephaloidophora communis* and *Gregarina valettei* in more detail; the former was also redescribed by Trégouboff (1912) and by Tuzet and Ormières (1964).

physiology of the developing barnacle larvae. Apparently, in some unknown way, the infection causes a delay in the liberation of the nauplii; the latter, however, continue to develop within the mantle to a physiological state that shortens the transformation time into the second naupliar stage during its free existence.

Trematoda

As may be noted from Table II, the metacercariae of only three species of digenetic trematodes of the family Microphallidae have been reported in barnacles. Lebour (1908-1911) was apparently the first to describe metacercariae from a species of barnacles on the Northumberland coast of England, which she named *Cercaria balani.* More recently, Ouspenskaia (1960) reported similar type metacercarial cysts in *Balanus balanoides* from the Barents Sea. However the description and figures are not detailed enough for us to make a comparison with our species, although they were described as the metacercariae of *Maritrema linguilla* (L. A. Jägerskiöld) and *Maritrema gratiosum* (W. Nicoll). The latter are sexually mature stages that occur in the intestine of gulls, terns and other marine birds.

In our routine studies on the biology of the barnacles, similar type metacercariae were also found in *Balanus balanoides* collected in local waters. The worms are contained in thin-walled, yellowish, more often white, and refringent spherical cysts measuring 0.3 mm in diameter; the body wall of the parasite is covered with delicate spines, except for its posterior third; oral and ventral suckers are approximately of equal size; the cecae are relatively long, each branch measuring on the average 0.5 mm in length, and easily demonstrated when stained vitally with neutral red (Pl. I, figs. 2-4). Attempts at excystment by feeding isolated cysts to killifish, *Fundulus heteroclitus*, were unsuccessful. Further experiments to induce this process were dropped in view of the failures reported by Hadley and Castle (1940) when they fed cysts from infested *Balanus balanoides* collected from Woods Hole, Massachusetts, and from the coast of Maine to young *Larus argentatus, Sterna hirundo hirundo, Trigonoides macularius*, white mice, white rat, kitten, and domestic fowl. On the basis of circumstantial evidence, *i.e.*, the discovery of sexually mature adults together with metacercarial cysts in the intestine of the turnstone, *Arenaria intrepes morinella*, a bird that is known to feed on barnacles, Hadley and Castle concluded that the metacercariae and the adults were the same; they considered this to be a new species for which the name *Maritrema arenaria* was given. The striking similarities of our form with those figured by Hadley and Castle lead us to conclude that the cysts from *Balanus balanoides* taken from local waters are also the metacercariae of *Maritrema arenaria.*

The pathological effects of metacercarial infestations in barnacles are not too well known. Our observations show that in light infestations, the cysts are usually localized on or near the gut; when the infestations are exceptionally heavy, all parts of the body, except for the appendages and the lumen of the gut are involved. In such instances, the metacercariae are firmly embedded in a relatively thick connective tissue formed around the external gut wall. Barnacles showing such extreme conditions have ovaries that are reduced to filiform cords of follicular tissue and entirely devoid of oocytes. Whether or not this is a consistent pathological feature remains to be established.

Table II

Trematoda

Host and Locality	*Parasite*	*Author*
Balanus sp. (Northumberland coast)	*Cercaria balani* (metacercariae)	Lebour, 1908/11
B. balanoides (Woods Hole)	Metacercariae of *Maritrema arenaria*	Hadley and Castle, 1940
B. balanoides (Barents Sea)	Metacercariae of *Maritrema gratiosum* W. Nicoll	Ouspenskaia, 1960
B. balanoides (Barents Sea)	Metacercariae of *Maritrema linguilla* L. A. Jägerskiöld	Ouspenskaia, 1960
B. balanoides (Coney Island)	Metacercariae of undetermined *Microphallidae;* in all probability *Maritrema arenaria*	Arvy and Nigrelli (present paper)

Isopoda

Infestations of barnacles by the protandrus hermaphrodite *Hemioniscus balanus* (Crustacea: Isopoda: Ipicaridea: Hemioniscidae) have been known since the latter part of the 19th century and have since been reported in these hosts from various parts of the world. In its developmental cycle, the males (cryptoniscus stage) become transformed into females when they take up the parasitic existence. The female is accompanied by grotesque changes in form, eventually becoming an enlarged star-shaped egg-sac (abdomen), with evidence of its crustacean characteristics indicated by the retention of certain head and thoracic appendages. In the early stages of the transformation processes, the parasitic female sucks the body fluids of the barnacle, which are stored into two large "liver" lobes; this nutrient material is eventually transferred to the ripening eggs as reserve food material (see Wimpenny, 1966).

Each barnacle may harbor one or more parasitic females; Perez (1923) found as many as seven individuals in a single *Balanus balanoides*. It has been suggested that such a heavy infestation inhibits the development of the gonads as the result of mechanical pressure, or may actually cause a destruction of the ovaries. However, such ovariectomized barnacles are still capable of carrying on most life functions as indicated by the continued rhythmic movements of the cirri of the parasitized animals.

Fungus and Lichens

Three species of fungi have been reported as infecting barnacles. Two of them, namely *Didymella balani* and *Pharcidia marina* from the tests and shell of *Balanus balanoides* and *Chthamalus stellatus* were originally classified as ascomycetes by Hariot (1887) and Bommer (1891), but have since been recognized (Santesson, 1939) as marine lichens of the genera *Arthropyrenia* and *Didymella* (for clarification of the taxonomy, see Johnson and Sparrow, 1961).

The third species, *Lagenidium chthamalophilum* (Phycomycete), is a virulent fungal agent that was found to be the cause of an epizootic in 1957 in the barnacle *Chthamalus fragilis denticulata* from Beaufort, North Carolina, with an incidence that ranged from 12.5% to 100% (Johnson, Jr., 1958). This highly

Table III

Isopoda: *Hemioniscus balanus*

Species	*Locality*	*Author*
Balanus sp.	German coast, North Sea	Buchholz, 1886
Balanus sp.	Wimereux, French coast, English Channel	Caullery and Mesnil, 1899
Balanus improvisus	Gironde estuary, France	Perez, 1900
Balanus perforatus	Roscoff, Brittany, France	Perez, 1923
Balanus balanoides	Roscoff, Brittany, France	Prenant, 1923
Chthamalus stellatus	Roscoff, Brittany, France	Prenant, 1923
Balanus balanoides	Atlantic coast north to Tromsø (Norway)	Crisp, 1951
Balanus amphitrite	English estuaries	Crisp and Molesworth, 1951
Balanus sp.	South Africa	Sandison, 1954
Balanus balanoides	Southwest coast of England	Crisp and Southward, 1954
Balanus porcatus	?	Crisp, 1954
Chthamalus dalli	North American Pacific coast	Cornwall, 1955
Elminius modestus	?	Crisp and Davies, 1955
Balanus balanoides	Atlantic French coast	Crisp and Fischer-Piette, 1959
Balanus perforatus	?	Crisp and Patel, 1960
Eliminius modestus	Roscoff	Bourdon, 1963
Balanus balanoides	Roscoff	Bourdon, 1963
Balanus balanoides	Halifax area (New Scotland)	Crisp, 1968
Balanus balanus	From Labrador to Massachusetts	Crisp, 1968
Balanus glandula	Friday Harbor	Crisp, 1968
Chthamalus dalli	Friday Harbor	Crisp, 1968
Balanus balanus	Irish Sea, Faroe, Shetlands	Crisp, 1968
Balanus hameri	Irish Sea	Crisp, 1968

Remarks: Crisp (1968) states that barnacles such as *B. improvisus, B. algicola, Chthamalus dentatus,* and *Elminius modestus,* may also be parastilized by *Hemioniscus balani.* Forms such as *Verruca stroemia, Balanus crenatus, B. perforatus,* and *B. stellatus* are never infested; Perez (1900) has made a similar observation, *e.g.* in the Gironde estuary *Balanus improvisus* is heavily infested by *Hemioniscus balani* but *Chthamalus stellatus* are never parasitized; the reason of this apparent immunity remains unexplained.

TABLE IV
LICHENS AND FUNGUS

Host	Locality	Parasites	Author
		Lichen	
Chthamalus stellatus	test	*Didymella balani*	Hariot, 1887
Balanus balanoides	shell	*Pharcidia marina*	Bommer, 1891
		Fungus	
Chthamalus fragilis var. *denticulata*	ova	*Lagenidium chthamalophilum*	Johnson, 1958

pathogenic fungus infects the ova and apparently is specific for *Chthamalus fragilis*, since *Balanus amphitrite* in the same waters is resistant to infection both under natural and experimental conditions.

Johnson reported that the fungus develops in the ova of the barnacle at any time between gastrulation and the emergence of the nauplii; neither the released nauplii nor the somatic tissues are involved. The degree of infection varies with the stage of development of the egg mass. Thus, embryos with three or more appendage buds are most often infected; earlier stage embryos, i.e. with one or more appendage buds, are completely destroyed, leaving only clusters of egg membranes filled with fungus mycelium. Lamellae with more mature embryos apparently are more resistant, since some embryos escape invasion by the fungus and develop into normal nauplii. The infection is initiated by laterally biflagellate planonts that become transformed into spores when they settle on the egg. Within three minutes after attaching to the egg membrane, the spore protoplasm penetrates the membrane, increases in size into a hyphal rudiment, and grows along the embryo. The infection is visible as pallid grey or grey-green lamellae. The infection spreads rapidly through the entire cluster so that within two days all the embryos are invaded. There can be little doubt that *Lagenidium chthamalophilum* attacking the ova of the barnacle *Chthamalus fragilis* may have caused a reduction in population density of this species in Beaufort, North Carolina, during and after the epizootic. As pointed out by Johnson (1958), further studies are needed to establish the importance of this fungus. Studies must be undertaken on distribution and severity of infection; conditions favoring the development and spread of the infection; the factors responsible for host susceptibility; and, whether or not the epizootics are cyclic.

TURBELLARIA

Members of the genus *Stylochus*, sometimes called the oyster "leech," (Platyhelminthes: Turbellaria: Polycladia: Acotylea: Stylochidae) are predators occurring free or "encapsulated" (walled-off by chitinous secretions of the host) in oysters, barnacles, pangurid crabs, and in other invertebrates (see Hyman, 1951; Cheng, 1967). Those in the barnacles are usually found free or encapsulated on the internal wall of the opercular valves, and sometimes closely associated with the ovaries (Skerman, 1960). *Styloclus ellipticus*, which according to Loosanoff (1956) may be responsible for the destruction of large numbers of oysters on the flats at Milford, Connecticut, was found locally in a population of *Balanus eburneus* attached to *Mytilus edulis*. The worms were found free on the internal wall of the opercular valves or deep within the host on which they were feeding. There was no evidence that the flatworms were feeding on the *Mytilus*.

It has been estimated that a single oyster-inhabiting turbellarian lays about 22,000 eggs in a month, which at 28° C hatch in a few days into pelagic ciliated larvae, become transformed into adults in two months, live a free existence in the littoral zone for about a year, and eventually encysting in great numbers on all parts of the oyster spat, causing heavy mortality. It remains to be seen whether or not *Stylochus*

TABLE V
TURBELLARIA

Host	Predator	Author
Balanus sp.	*Stylochus neapolitanus*	Lang, 1884
Balanus sp.	*Stylochus zanbibaricus*	Skerman, 1960
Balanus eburneus	*Stylochus ellipticus*	Arvy and Nigrelli (present paper)

ellipticus is as important a predator for young, newly set barnacles as it is for the spats. The abnormal arrangement of the plates of *Balanus eburneus* attacked by the *Stylochus ellipticus,* which we observed, may be indicative of an invasion early in its growth.

Discussion

Much has been written on the biology of barnacles, especially on their distribution, nutrition and growth, factors affecting mortality of natural populations, and particularly the role of temperature on the life cycle. These topics have been reviewed by several authors (Henry; Bookhout and Costlow, Jr.; Connell; Barnes) in a symposium on "Marine Boring and Fouling Organisms" held at the Friday Harbor Laboratories in 1957 (edited by Dixy Lee Ray and published in 1959 by the University of Washington Press). Very little information is included on the enemies of barnacles; it is apparent from the present paper that more studies are needed to establish the possible role of predators, parasites, and diseases in barnacle ecology. It is possible that one or more of these agents, under certain specific conditions, may be important for the biological control of these economically significant fouling organisms. More studies are especially needed on possible fungal and bacterial infectious agents that may play such a role.

Summary

Three species of organisms previously reported as predators or as parasites of barnacles and two commensal peritrichs, have been found in populations of *Balanus eburneus* and *Balanus balanoides* occurring on the rock jetties from Sea Gate and immediately adjacent to the Osborn Laboratories at Seaside Park, Coney Island, New York City, respectively. The species found were *Cephaloidophora communis* (Protozoa: Sporozoa: Gregarinida: Eugregarinina: Cephalinoidea: Cephaloidophoridae) from the intestine of *Balanus eburneus; Epistylis horizontalis* and *Epistylis nigrellii* (Protozoa: Ciliophora: Ciliata: Peritrichidae) from the branchial lamellae of *Balanus balanoides* and *B. eburneus,* respectively; *Stylochus ellipticus* (Platyhelminthes: Turbellaria: Polycladia: Acotylea: Stylochidae) from the internal wall of the opercular valves of *Balanus eburneus* attached to *Mytilus edulis;* and metacercariae, possibly of *Maritrema arenaria* (Trematoda: Digenea: Microphallidae), on the external gut wall and other tissues of *Balanus balanoides.* The presence of these organisms in local barnacles represents a new geographical record. These and their effects on the host are briefly described together with a review of the literature on other parasites and diseases of barnacles.

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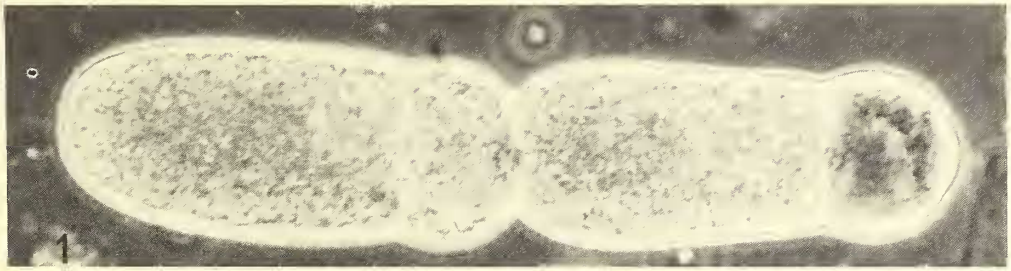
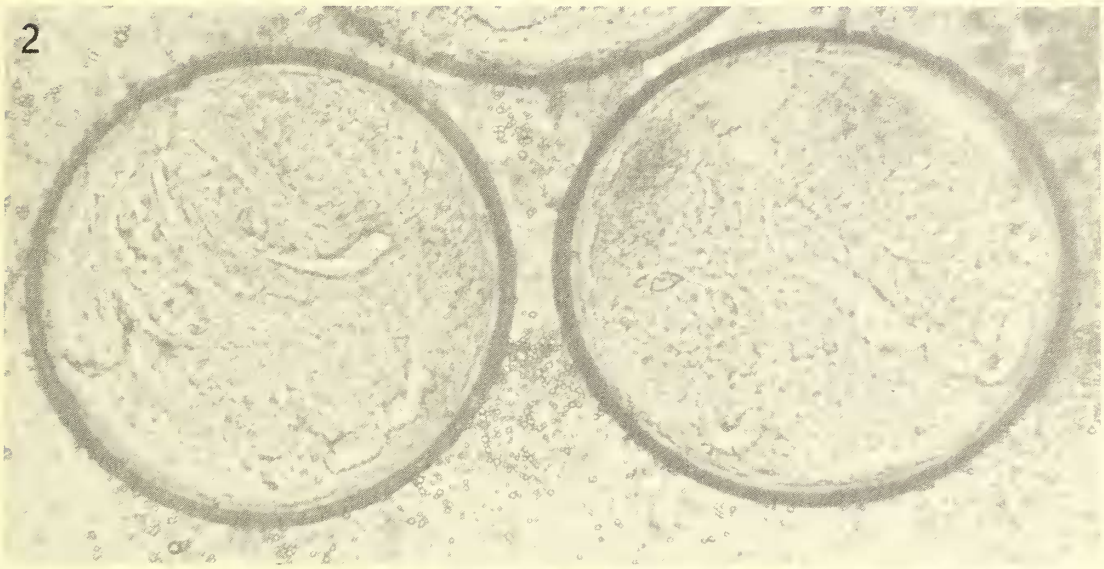
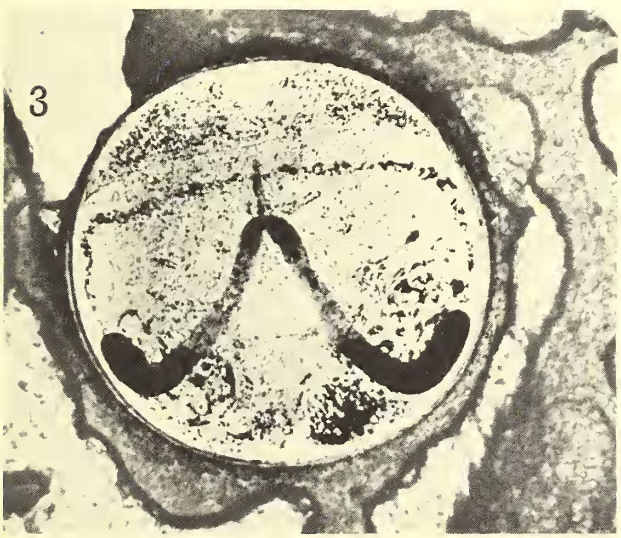
EXPLANATION OF THE PLATE

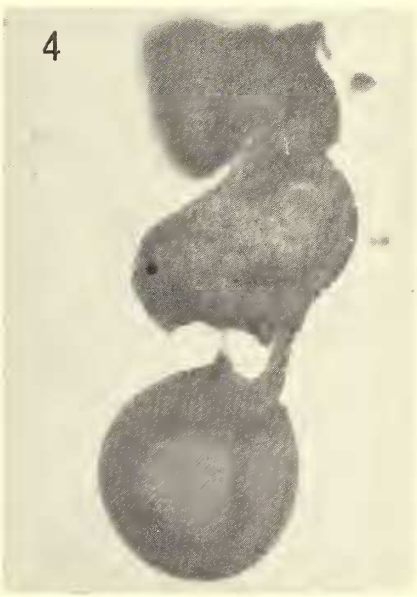
Fig. 1. Sporadin of *Cephaloidophora communis* Mawrodiadi (1908) from the intestine of *Balanus eburneus* collected on rock jetties adjacent to Sea Gate, Coney Island, Brooklyn, New York.

Figs. 2-4. Metacercariae of Microphallid digenetic trematode, probably *Maritrema arenaria* Hadley and Castle (1940), from *Balanus balanoides* collected on rock jetties on Coney Island Beach; Fig. 2: unstained living specimens; Fig. 3: cyst stained with neutral red; Fig. 4: excystment.









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